# ON THE USE OF THE ROBUST DESIGN WITH TRANSIENT CAPTURE–RECAPTURE MODELS

JAMES E. HINES, WILLIAM L. KENDALL, AND JAMES D. NICHOLS

United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland 20708, USA

ABSTRACT.—Capture—mark—recapture studies provide a useful mechanism for estimating the components of the population dynamics of birds, especially survival. In such studies, it is important that the population being captured matches the population of interest. In many studies, transients are captured along with the population of interest (e.g. resident breeders). Ignoring that phenomenon produces negatively biased survival estimates, because transients do not return. Although transients cannot be distinguished from residents in the hand, previous methods have adjusted for transience by relying on those captured in more than one year to provide direct estimates of survival rate for residents. Here, we extend that approach by supplementing that cohort of known residents with those previously unmarked birds captured twice or more, at least *d* days apart, within a season. We provide an *ad hoc* approach to that extension in detail and outline two more formal approaches. That extension increases the precision of survival estimates. *Received 1 January 2003, accepted 23 July 2003*.

Resumen.—Los estudios de captura, marcado y recaptura representan un mecanismo útil para estimar los componentes de la dinámica poblacional de las aves, especialmente la supervivencia. En ese tipo de estudios, es importante que la población que está siendo capturada coincida con la población de interés. En muchos estudios, se capturan individuos transeúntes junto con los individuos pertenecientes a la poblacion de interés (e.g. residentes reproductivos). Ignorar este fenómeno genera un sesgo negativo en la estimación de la supervivencia, debido a que los individuos transeúntes por definición son aquellos que no regresan. A pesar de que los individuos transeúntes no pueden ser diferenciados de los residentes cuando son capturados, ciertos métodos permiten determinar la presencia de transeúntes considerando sólo aquellos individuos capturados en más de un año, lo que permite obtener estimaciones directas de la tasa de supervivencia de los residentes. En este trabajo, extendemos este método suplementando la cohorte de residentes conocidos con aquellas aves no marcadas previamente pero capturadas dos o más veces durante una estación, con por lo menos d días de separación. Brindamos un enfoque ad hoc detallado de dicha extensión y describimos dos enfoques formales más. Esta extensión aumenta la precisión de las estimaciones de supervivencia.

Probabilistic Capture—recapture models for open populations have been used to estimate avian survival rates for some time (e.g. Cormack 1964, Carothers 1979). A common sampling design is to capture and recapture or resight birds during a short period each year (e.g. during the breeding season) for multiple years to estimate annual survival rate. A long-standing problem in application of capture-recapture models to such data involves the issue of transient individuals that are just passing through the sample area at the time of sampling but that have no chance of returning in subsequent years. Standard Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992) assume that all animals alive at

Existence of transients produces a type of capture-history dependence (Williams et al. 2002), in that previously marked birds are residents by definition and include no transients. However, unmarked birds are expected to exhibit a lower probability of apparent survival until any subsequent sampling period, because they represent a mix of residents and transients (which by definition do not return). Pradel et al. (1997) dealt with the transient problem in

sample period *i* have the same chance of apparent survival (i.e. surviving and remaining in the population) until any subsequent sampling period, and of being captured or resighted during any period *j*, given that they are alive and in the population. Existence of transients violates that assumption, because that subset of birds does not return to the study area and therefore has no chance of being seen again.

 $<sup>^1\</sup>mbox{Address}$  correspondence to this author. E-mail: william\_kendall@usgs.gov

open population capture–recapture models through use of a mixture model for survival of unmarked animals (see below). That approach has seen substantial use in capture–recapture studies of avian populations (e.g. Loery et al. 1997, DeSante et al. 1999, Rosenberg et al. 1999, Spendelow et al. 2002).

Annual avian sampling periods sometimes cover relatively long periods of time (e.g. two months). Depending on the details of sampling, sometimes those long periods can be viewed as containing multiple secondary sampling periods, corresponding to the robust design of Pollock (1982). In such cases, there may be ancillary data providing evidence about residence status of birds. A bird may be captured multiple times during the period; and if there is sufficient time separating those captures, then it can be inferred that the individual is a resident. Other analysts have used that extra information in various ways to help estimate survival rates (e.g. Buckland and Baillie 1987, Peach et al. 1990). Here, we consider ways to incorporate that extra information about residence status resulting from the robust design into open population capture-recapture models of the type developed by Pradel et al. (1997) to deal with transients.

# PRADEL'S TRANSIENT MODEL

The transient model of Pradel et al. (1997) was developed for open-population data in which an animal is either captured or not at each sampling period. That model is perhaps best developed by considering four sets of potentially time-specific parameters:  $\phi_i$  is the probability that a resident bird present at time (year) i is still alive and in the population at time i + 1;  $\phi_i^t$ is the probability that a transient bird present at time *i* is still alive and in the population at time i + 1;  $\tau_i$  is the probability that an unmarked bird captured and released at time i is a transient;  $p_i$ is the probability that a bird alive and resident in the population at time *i* is captured. Although  $\phi_i$  and  $\phi_i^t$  represent apparent survival probabilities (i.e. the complement of which is death or permanent emigration), we will refer to them subsequently as survival probabilities. The logic underlying that model is most easily conveyed by writing out the probabilities of exhibiting particular capture histories. A capture history is simply a vector of *K* ones and zeros, where *K* 

denotes the number of sampling occasions (e.g. years) in the study, that is, a "1" indicates that the bird was captured at a particular occasion and a "0" indicates that the bird was not captured at an occasion. So a history of (0 1 0 1 1) indicates an animal that was not captured the first or third occasions of a five-period study but was captured at occasions 2, 4, and 5.

To illustrate the logic underlying the Pradel et al. (1997) model, consider the following two capture histories and their associated probabilities:

$$P(1\ 1\ 0\ 1\ |\ \text{release in period}\ 1) = (\tau_1 \varphi_1^t + [1 - \tau_1] \varphi_1) p_2 \varphi_2 (1 - p_3) \varphi_3 p_4$$
  
 $P(0\ 1\ 0\ 1\ |\ \text{release in period}\ 2) = (\tau_2 \varphi_2^t + [1 - \tau_2] \varphi_2) (1 - p_3) \varphi_3 p_4$ 

Note that in both of the above capture histories, survival following initial capture is a mixture of survival rates of transients,  $\varphi_i^t$ , and residents,  $\varphi_i^t$  with  $\tau_i$  being the associated mixture parameter. However, survival probability for subsequent capture periods is simply given by the resident survival parameter,  $\varphi_i^t$ . Estimation under the above general model is not possible. However, Pradel et al. (1997) defined a transient as an animal with probability of returning to the area equal to 0,  $\varphi_i^t = 0$ . Under that natural constraint, the above capture-history models reduce to the following:

$$P(1\ 1\ 0\ 1\ |\ \text{release in period}\ 1) = (1 - \tau_1)\varphi_1p_2\varphi_2(1 - p_3)\varphi_3p_4$$
  
 $P(0\ 1\ 0\ 1\ |\ \text{release in period}\ 2) = (1 - \tau_2)\varphi_2(1 - p_3)\varphi_3p_4$ 

During the first occasion, all animals are unmarked, and only the product of the proportion resident and resident survival probability,  $(1 - \tau_1)\phi_1$ , can be estimated. However, during subsequent periods, both  $\tau_i$  and  $\varphi_i$  can be estimated separately. For example, consider animals released in period 2 in the above two capture histories. In the first capture history, animals released in period 2 are already marked and thus known to be residents, and the subsequent (after occasion 2) portion of the capture history provides the information needed to estimate  $\phi_2$ . That information about  $\phi_2$  then permits decomposition of the product  $(1 - \tau_2)\phi_2$  in the model for the second capture history and thus permits estimation of  $\tau_2$ .

A Transient Model under the Robust Design

The robust design of Pollock (1982) includes multiple (*l<sub>i</sub>*) secondary periods within each primary period i. For example, assume a primary trapping occasion that extends for seven weeks during the breeding season each year and further assume that actual sampling of birds occurs during weeks 1, 4, and 7. Those would be viewed as the  $l_i$  = 3 secondary sampling periods. There are multiple ways to consider the modeling of capture–recapture data across those secondary periods. Below, we consider the sampling situation in which the sampled population of residents is closed within each season, so that no residents enter or leave the sampled area during the primary sampling period. We outline an ad hoc approach and a likelihood approach.

Ad hoc *approach*. — The simplest approach for using capture-recapture data within a primary period involves identification of a resident as any bird that is recaptured some minimum period of time following initial capture. For example, assume that a bird remaining on the study site for at least d days (e.g. d = 10) is definitely a resident. Thus, for the above example of secondary sampling every three weeks, any bird captured on more than one secondary sampling occasion would be identified as a resident. That extra information can be used to categorize some new birds (not captured in a primary period before period i) as residents. That categorization leads to two kinds of new releases, residents and unknowns. Under the model of Pradel et al. (1997), all new birds were viewed as unknowns, and their first-year survival thus modeled using the mixture parameterization,  $(1 - \tau_i)\phi_i$ . Under the simple robust design model, new birds that are not recaptured more than d days following initial capture are categorized as unknowns and modeled just as in Pradel et al. (1997). However, new birds that are recaptured following d days are categorized as residents and given the same survival probability as birds caught in previous years,  $\phi_{i}$ .

To illustrate that modeling, consider the capture histories presented above, but now consider two groups of birds with each capture history, those recaptured more than *d* days following initial capture during the primary period of initial capture (released as residents) and those not recaptured more than *d* days following initial capture (released as unknowns):

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P(1\ 1\ 0\ 1\ |\ \text{release in period 1 as unknown}) = \\ (1-\tau_1')\varphi_1p_2\varphi_2(1-p_3)\varphi_3p_4 \\ P(1\ 1\ 0\ 1\ |\ \text{release in period 1 as resident}) = \\ \varphi_1p_2\varphi_2(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release in period 2 as unknown}) = \\ (1-\tau_2')\varphi_2(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release in period 2 as resident}) = \\ \varphi_2(1-p_3)\varphi_3p_4
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where  $\tau_i'$  is the probability that a bird unmarked before period i and captured and released only once or less than d days apart within period i is a transient. Note that the above capture histories still retain a single entry (captured at least once or not caught) for each year.

Several comments should be made about that parameterization. First, note that this simple use of the extra information provided by recaptures requires no additional parameters. The model requires no real modeling of the recapture data within a season and simply uses the data to reclassify some new animals from unknown status to known resident status. Second, the definition of the transient parameter,  $\tau_i'$ , is slightly different from  $\tau_i$ . Under the parameterization of Pradel et al. (1997),  $\tau_i$  can be viewed as the proportion of all newly captured birds (not previously marked) at time *i* that are transients. Under the robust design approach, τ' applies only to the new birds that were not recaptured in another secondary period more than d days after initial capture. The robust design reduces uncertainty in that the group of unknown-status birds to which  $\tau_i'$  applies is smaller (there are fewer unknowns and therefore  $\tau' \geq \tau$ ) than in the case where such extra information about resident status is not used. A third point involves identifiability of model parameters. As noted above, under the original model of Pradel et al. (1997), the product,  $(1-\tau_1)\phi_1$ , can be estimated, but the separate survival,  $\phi_{1}$ , and transient,  $\tau_{1}$ , parameters cannot. In the model of Pradel et al. (1997), there is no group of known residents in the first sampling period from which information about  $\phi_1$  can be obtained. In contrast, the robust design does provide a group of known residents (those recaptured more than d days after initial capture), permitting estimation of  $\phi_1$  and hence  $\tau_1$ .

That approach has been implemented in TMSURVIV (see Acknowledgments) and has been used with North American landbird capture–recapture data resulting from the

monitoring avian productivity and survivorship (MAPS) program (Nott and DeSante 2002). In the analyses of Nott and DeSante (2002), the ad hoc robust design approach described here yielded similar estimates of annual survival and capture probabilities as the open-model approach of Pradel et al. (1997), as expected. Proportions of new unmarked individuals estimated to be transients ( $\hat{\tau}_i'$  using the above notation, which differs from that of Nott and DeSante 2002) tended to be larger under the robust design. That difference was expected as the transient parameters under the two approaches differ, with  $\hat{\tau}_i$  corresponding to a smaller group under the robust design (unmarked birds not captured twice >10 days apart, rather than all unmarked birds). Precision of the estimated survival and recapture probability parameters was better under the robust design. Specifically, the CV of survival estimates improved by an average of 16.2% (range of 1.3 to 29.3%) across 10 passerine species (Nott and DeSante 2002). That increased precision was also expected, as the ability to classify additional unmarked birds as residents reduces uncertainty by increasing the number of known residents and reducing the size of the group of animals to which the mixture model applies.

Likelihood approach.—A second approach to using the robust design in transient models would be to follow a likelihood approach similar to that developed by Kendall et al. (1995, 1997) for standard capture-recapture models. Under that approach, captures and recaptures occurring over the secondary sampling periods within each primary period would also be modeled. Consider the situation where resident animals are available at the sampled location for the duration of the primary sampling period (residents are available for capture at each of the l, secondary sampling periods). Sampling thus begins after breeding has been initiated and ends well before residents begin moving away to nonbreeding areas.

Modeling of the secondary period capture-history data requires a more detailed description of data than the open-model capture-history notation defined above. We again use "1" to denote a capture and "0" to denote no capture, but now we must use that notation to describe secondary sampling periods (e.g. see Williams et al. 2002). Consider the robust design capture history 101 001. That history shows two primary sampling

periods of three secondary occasions each. In primary period 1, the animal was caught on secondary occasions 1 and 3, but not on secondary occasion 2. In primary period 2, the animal was not caught in either secondary occasion 1 or 2, but it was caught in secondary occasion 3.

Modeling of the data over secondary occasions requires only capture probability and proportion transient parameters (for each secondary period, j) and relies on closure (i.e. no ingress or egress) of the resident population for the duration of sampling for each primary period i:  $p_{i,j}$  is the probability that a bird alive and present in the population at secondary occasion j of primary period i is caught;  $\tau_{i,j}$  is the probability that an unmarked bird present at secondary occasion j of primary period i is a transient. If we retain the survival notation of the Pradel et al. (1997) model, then we can model example capture histories as follows, conditioning on first capture:

 $\begin{array}{l} P(101\ 001\ |\ release\ in\ secondary\ occasion\ 1\\ of\ primary\ occasion\ 1\ as\ unknown) =\\ (1-\tau_{1,1})(1-p_{1,2})p_{1,3}\varphi_1(1-p_{2,1})(1-p_{2,2})p_{2,3}\\ P(010\ 101\ |\ release\ in\ secondary\ occasion\ 2\\ of\ primary\ occasion\ 1\ as\ unknown) =\\ (1-\tau_{1,2})(1-p_{1,3})\varphi_1p_{2,1}(1-p_{2,2})p_{2,3}\\ P(011\ 000\ |\ release\ in\ secondary\ occasion\ 2\\ of\ primary\ occasion\ 1\ as\ unknown) =\\ (1-\tau_{1,2})p_{1,3}([1-\varphi_1]+\varphi_1[1-p_{2,1}][1-p_{2,2}][1-p_{2,3}])\\ P(010\ 000\ |\ release\ in\ secondary\ occasion\ 2\\ of\ primary\ occasion\ 1\ as\ unknown) =\\ \tau_{1,2}+(1-\tau_{1,2})(1-p_{1,3})([1-\varphi_1]+\varphi_1[1-p_{2,1}]\\ [1-p_{2,2}][1-p_{2,3}]). \end{array}$ 

The first three capture histories above are known to represent residents (hence contain only a term,  $1-\tau_{1,j}$ ), either because the animals were caught twice within primary period 1 (first and third histories) or because they were caught in primary period 2 (second history). The fourth animal was caught only once and was not known to have been a resident. Thus, that history is modeled with a mixture that includes the possibility that the animal is  $(\tau_{1,2})$  and is not  $(1-\tau_{1,2})$  a transient.

We note that although the *ad hoc* approach required the same number of parameters as the open model of Pradel et al. (1997), the above approach requires extra parameters corresponding to capture probabilities and transient proportions for each secondary sampling period.

Although we have not conducted a formal comparison, the smaller number of parameters associated with the *ad hoc* approach is appealing. We also note that once again, the interpretation of the period-specific transient parameters differs from that of the transient parameters of the preceding two approaches (see above definitions).

Open modeling over secondary periods.—Under some sampling situations, gains and losses of animals occur between secondary sampling periods within a primary period. In such situations, open models can be developed for the secondary periods (Schwarz and Stobo 1997, Kendall and Bjorkland 2001). We believe that such models can be adapted to deal with transients as well. Such models will be similar to the above model presented for the case of closure over secondary periods, but they will contain additional survival parameters,  $\phi_{i,i'}$  corresponding to the probability that a resident animal present in secondary period *j* of primary period i will still be present at secondary period j + 1, where  $i < l_x$ . They will also contain parameters that describe probability of entry to the study area. Such models would again have capture and transient parameters for each secondary period as for the closed model case presented above. We present no details of such modeling, because we have doubts about how useful such models will be for estimating survival. Given the increase in number of parameters, it may well be that the ad hoc approach presented initially will provide the best way to use robust design data to estimate survival while accounting for transients.

# Discussion

Pradel et al. (1997) motivated their transient modeling by noting that transient individuals seemed to occur frequently in the sampling of birds and small mammals, and that failure to deal with such individuals produced survival rates that were not appropriate for resident individuals. Their mixture model approach provides a reasonable way to deal with the presence of transients when estimating survival rate. Users of those transient models for bird populations (D. F. DeSante in particular) have suggested the desirability of incorporating in such models additional information resulting from robust sampling designs. The work reported here is a response to that request. We

have considered different ways of using the additional data and have written software to implement the *ad hoc* approach described above (see Appendix 1). Nott and DeSante (2002) have used that new modeling approach and indeed obtained increased precision on parameter estimates.

Our work relies on an assumed minimum residence time of d days to determine whether an individual bird is a resident or transient, on the basis of knowledge about the species. We envision two approaches to assure the veracity of that assumption. The simplest approach is simply to be conservative. If d is too small, then transients will be misclassified as residents, thus inducing unknown negative bias in the estimation of  $\phi_i$ . However, if d is too large, it results not in misclassification, but more previously unmarked birds will remain in unknown status. Therefore, it does not induce bias but does reduce the benefit to precision of incorporating within-season recaptures. That reduction in precision is measurable. Simulation could be informative for balancing bias and precision using something like mean-square error as a criterion for determining the appropriate value of *d*.

The second approach is to evaluate *d* by direct modeling, allowing for the possibility that some of those designated as residents on the basis of *d* could be transients. That modeling approach is outlined in Appendix 2. The hypothesis that all birds assigned to resident status on the basis of *d* are residents can be evaluated using model selection or averaging (Burnham and Anderson 2002), or direct hypothesis testing as in Skalski and Robson (1992) or MacKenzie and Kendall (2002). The latter uses equivalence testing, which would make it more difficult to conclude that all birds assigned to resident status are indeed residents.

The approaches described above are mixture models, just as are the models of Pradel et al. (1997). We emphasize that such models incorporate extra parameters and associated uncertainty, when compared to models that ignore transients. That observation leads to the recommendation that, whenever possible, modifications of study timing and design are better ways to deal with transients than modeling (also see Cilimburg et al. 2002). For example, if a time period can be identified when a studied population is reasonably certain to include only resident animals, then it is preferable to sample

at that time and avoid the need for transient modeling. The models presented by Pradel et al. (1997) and above are simply intended for use with populations for which it is not possible to identify sampling periods during which only residents are available.

We also note that the sole purpose of the above models is to provide estimates of resident survival that are not influenced by the existence of unknown numbers of transients. The transient parameters  $(\tau_i, \tau_i', \tau_i)$  frequently will not be of interest, as they reflect both biology and such aspects of sampling as magnitude of capture probability and proximity of sampling period to the beginning of the study. For example, higher capture probabilities will result in higher proportions of residents being marked and thus in larger proportions of unmarked animals being transients. We also expect smaller proportions of transients among unmarked animals at the beginning of a study, when relatively smaller proportions of resident animals will have been marked. The design-dependence of the interpretation of the transient parameters is emphasized by the different interpretations noted for those parameters under the models of Pradel et al. (1997), the ad hoc robust design approach presented above, and the above likelihood-based approach for the robust design.

None of the transient models described here includes parameters that represent the proportion of animals that use an area in a given year that are transients. Although  $\tau_i$ ,  $\tau_i'$ , and  $\tau_{i,j}$  describe the proportions of unmarked animals captured at a given time that are transients, estimating the proportion of the population that is unmarked at that time is implied to estimate the proportion of the population that is transient. Estimation of such a parameter is sometimes possible with the robust design, but such estimation will depend on specifics of the study design as well as on assumptions about the arrival and departure patterns for transients and residents within the year.

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## Appendix 1

### Computer Implementation

Estimates of the parameters described above can be obtained using software specifically written to handle that type of data (TMSURVIV), or using a general-purpose capture—recapture analysis program (MARK; White and Burnham 1999). Originally written to compute estimates under the Pradel et al. (1997) model, a slight modification of TMSURVIV allows the input of the extra information required for the *ad hoc* approach. By default, TMSURVIV uses the Pradel model. If the input data file contains a field indicating the resident status of each animal and a control statement, TMSURVIV will compute estimates using the *ad hoc* approach. The following text shows an example input file for TMSURVIV with *ad hoc* approach modifications shown in italics:

Individuals that were captured more than d days apart in their first primary capture period are denoted with r after the history (in column 6). Those records will be treated as known "residents" by the program, whereas records without the r will be treated as "unknown." The transient parameter output from TMSURVIV in that case would be the proportion of "residents" of the "unknown" group.

The same results could be obtained using program MARK by treating the known residents (animals caught at least two times separated by at least d days in the first primary capture occasion) as group 1, and the unknown animals as group 2. Parameter indices for capture-probability would be equal for the two groups. Parameter indices for survival would be different for the first occasion after release (matrix diagonal), then equal (across groups) for all other occasions. Although MARK will not compute  $\hat{\tau}_i'$  directly, it can be computed by dividing the survival rate estimate for the first year after release (diagonal) for the unknown status group by the corresponding survival rate estimate for the known resident group.

For example, for a four-year study, the survival parameter indices in MARK for resident (group 1)

and unknown status birds (group 2), respectively, would be:

	Resident			Unknown status			
1	2	3	4	2	3		
	2	3		5	3		
		3			6		

#### APPENDIX 2

#### EVALUATING CRITERION d FOR RESIDENCY

Uncertainty could exist about the appropriateness of d, the minimum number of days between encounters of a bird that would designate it as a resident. If d is chosen to be too large, that would decrease the precision of survival estimates but not bias them. If d is too small, however, that would assign some transients to resident status and thus negatively bias survival estimates. A candidate value for d could be evaluated through modeling, by first defining  $\tau_i^{\prime\prime}$  as the probability that a bird—first marked in year i and observed in that year at least twice more than d days apart—is a transient. We can then rewrite the capture-history probabilities from the ad hoc robust design section above as

$$P(1\ 1\ 0\ 1\ |\ \text{release in period}\ 1\ \text{as unknown}) = \\ (1-\tau_1')\varphi_1p_2\varphi_2(1-p_3)\varphi_3p_4 \\ P(1\ 1\ 0\ 1\ |\ \text{release in period}\ 1\ \text{as suspected resident}) = \\ (1-\tau_1'')\varphi_1p_2\varphi_2(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release in period}\ 2\ \text{as unknown}) = \\ (1-\tau_2')\varphi_2(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release in period}\ 2\ \text{as suspected resident}) = \\ (1-\tau_2'')\varphi_2(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release in period}\ 2\ \text{as suspected resident}) = \\ (1-\tau_2'')\varphi_2(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release in period}\ 2\ \text{as suspected}) = \\ (1-\tau_2'')\varphi_2(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release in period}\ 2\ \text{as suspected}) = \\ (1-\tau_2'')\varphi_2(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\ (1-\tau_2'')\varphi_3(1-p_3)\varphi_3p_4 \\ P(0\ 1\ 0\ 1\ |\ \text{release}) = \\$$

Parameters 1 to 3 represent  $\phi_1$ ,  $\phi_2$ , and  $\phi_3$ , and parameters 4 to 6 represent  $(1 - \tau_1')\phi_1$ ,  $(1 - \tau_2')\phi_2$ , and  $(1 - \tau_2')\phi_3$ . If desired,  $\tau_1'$  can then be estimated as:

$$\hat{\tau}_{1}{'} = 1 - \frac{\text{estimate of parameter 4}}{\text{estimate of parameter 1}}$$

If  $\tau_i'' = 0$ , that would indicate all suspected residents were indeed residents and support the choice of d. If  $\tau_i'' = \tau_i'$ , then there would be no distinction between suspected residents on the basis of d, and those unmarked birds encountered only once in a given year. Either of those questions can be evaluated for a given data set. For example, in MARK the survival parameter indices presented above can be modified accordingly:

Susp	Suspected resident			Unknown status			
3	1	2	6	1	2		
	4	2		7	2		
		5			8		

Notice that the parameters on the diagonal are unique for each group. To evaluate  $\tau_i''=0$ , one would set parameters 4 and 5 equal to parameters 1 and 2, respectively. To evaluate  $\tau_i''=\tau_i'$ , one would set parameters 3, 4, and 5 equal to parameters 6, 7, and 8, respectively. That evaluation could be conducted using model selection or averaging based on AIC (Burnham and Anderson 2002), or through traditional hypothesis testing (Skalski and Robson 1992) or equivalence testing (MacKenzie and Kendall 2002). If results indicate that  $\tau_i''$  are distinct, survival rate can still be estimated in the face of that. However, to avoid estimating extra parameters, one should consider choosing a larger value for d.